The use of *Espeletia* by paramo hummingbirds in the Eastern Andes of Colombia

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Above the upper limit of woodland in the northern half of the Andes are extensive tracts of open moorland characterised by tussocky plants, many of which have their leaves arranged in "rosettes". The climate is cool and very wet. This zone of vegetation, generally known as the páramo, extends from c. 3200 m (the lower limit varying according to local conditions) up to the snowline. Vuilleumier & Simberloff (1980) discuss the definition of the term "páramo" from an ornithological point of view, and give botanical details; see also Cleef (1981). Three divisions are sometimes recognised: the subpáramo at lower levels, where there is a significant admixture of bushy plants; the typical páramo, mainly between 3400 and 4200 m; and the superpáramo at higher levels, where the vegetation is sparse and much rock and gravel remains exposed.

Among the many plants peculiar to the páramo, the genus *Espeletia* (family Compositae) is outstanding. The entire genus, consisting of some 80 species, is confined to the páramos of northwestern Venezuela, Colombia and northern Ecuador. Espeletias are not found on all the páramos in this area, being absent, for instance, from the greater part of the Western Andes of Colombia and from the Santa Marta massif; but where they occur they tend to be the most massive and conspicuous element in the vegetation, dominating miles of open moorland. They vary in size, but all have much the same form. The leaves grow in a rosette, starting at ground level in young plants. The old leaf bases are persistent, so that in older plants a "trunk" is formed, which in the largest species may be up to 3 m high but in most is not more than about 1 m. The long-stalked inflorescences, bearing yellow flowers like small sunflowers, grow from the middle of the rosette of leaves. The leaves and all parts of the inflorescences except the petals and flower discs are covered with a layer of whitish "wool", giving the plants, and the landscape in which they occur, a silvery appearance. Open flowers tend to be obliquely pendent, but may be orientated at all angles from horizontal to fully pendent. They do not produce nectar, and are probably pollinated mainly by bumble bees (*Bombus* spp.) which visit them to collect pollen.

The greatest concentration of *Espeletia* species occurs in the Eastern Andes of Colombia and adjacent parts of northwestern Venezuela (17 species in Boyacá and 11 species in Cundinamarca, Colombia; 10 species in Venezuela—Cuatrecasas 1979). Only 2 species occur in the central cordillera of northern Ecuador, and there is an isolated colony of 1 species at 1° S in Ecuador. Vegetation of páramo type, however, extends a good deal further south, reaching its southern limit at 8° S in Peru. Further south, from Peru through Bolivia to Argentina and Chile, páramo gives place at high altitudes above the tree line to the puna, a floristically very different kind of vegetation adapted to more arid conditions and greater extremes of temperature.

Between 1 August and 11 September 1982 I had an opportunity to carry out a limited field study (a total of 41 hours on 8 days) of the páramo hummingbirds of the Eastern Andes of Colombia. Most observations were made

on the Páramo de Chisacá, c. 40 km SSW of Bogotá, at altitudes of 3450–3900 m. This is a spur of the extensive highland area generally known as the Páramo de Sumapaz. Briefer observations were also made on small patches of páramo on the mountains behind Bogotá, at altitudes of 3000–3200 m. In all these areas the espeletias were in full flower at the time of my visits.

The hummingbirds

Six species of hummingbirds were recorded foraging on the páramo in the Chisacá area: *Oxypogon guerinii, Chalcostigma heteropogon, Ramphomicron microrhynchum, Lesbia victoriae, Pterophanes cyanoptera* and *Colibri coruscans*. This appears to be the complete list of species which can be expected at high altitudes on the páramo de Sumapaz. A few others, such as *Eriocnemis vestitus* and *Aglaeactis cupripennis,* range up to the subpáramo—the former was common in such areas in the mountains behind Bogotá—but they do not, apparently, normally occur above this zone.

Pterophanes cyanoptera and *Colibri coruscans* were not associated with the espeletias; on the páramo they were seen only where large ground bromeliads of the genus *Puya* were in flower. *Pterophanes cyanoptera* is a very large hummingbird (wing up to 115 mm) with a long bill (c. 30 mm). It is probably a *Puya* flower specialist; its bill is well adapted to the corollas of the 2 species of *Puya* at which it was seen feeding (corolla tubes 35 and 39 mm). It was also seen feeding at the flowers of a mistletoe, *Aetanthus holtonii,* growing on small trees bordering open páramo. *Colibri coruscans* is a fairly large (wing c. 77 mm, bill 24 mm), ecologically adaptable species with a wide altitudinal range in Colombia and elsewhere in the Andes.

The 4 other species were closely associated with espeletias. They are small or medium-sized hummingbirds with short, straight and sharply pointed bills. *Ramphomicron* has the shortest bill of any hummingbird (c. 7 mm), while the bills of *Oxypogon* and *Chalcostigma* are very short for their size (c. 8.5 and 11 mm, respectively). These 3 species all have rather long tails. *Oxypogon* and *Chalcostigma* have unusually long legs and large, strong feet for hummingbirds (Dorst 1956, Carpenter 1976). The combination of short bill, long tail and long legs gives them a distinctive appearance, more like a small passerine bird than a typical hummingbird. *Lesbia* males have extremely long tails, and females much shorter tails that are still very long compared with most hummingbirds.

Exploitation of espeletia flowers

It soon became obvious that the flowers of espeletia were providing a major part of the food of all 4 of the short-billed hummingbirds. Their behaviour was so similar that the same account may apply to all of them. A bird feeding at espeletia flowers would either perch on a lower flower-head and stretch upwards to the one above, or cling to the flower-head (if necessary beating its wings to maintain its position); or, if neither of these courses was possible, it would hover close to it in typical hummingbird fashion. When in position, it probed the flower disc repeatedly and thoroughly, before moving on to an adjacent flower-head and repeating the process. In this way it would work through a clump of plants, more or less systematically visiting all the open flowers. Because of the density of the espeletias, it was usually not possible to watch a bird throughout the whole of a feeding

bout, but it was common for bouts to last for 3 or 4 minutes, in the course of which 20 or 30 flower-heads would be visited.

I had no evidence that the hummingbirds were taking pollen from the flowers. Thus I never saw hummingbirds with pollen coating their forehead and chin, as Carpenter (1976) described for the high-altitude hummingbird *Oreotrochilus estella,* which eats the pollen and at the same time pollinates the composite *Chuquiraga spinosa* in Peru. On the other hand the probing behaviour strongly suggested that they were seeking food hidden in the interstices of the flower disc, and this interpretation is supported by other considerations. Espeletia flowers support very large populations of small phytophagous insects, whose numbers increase as the flowering period advances (Sturm 1979). From a sample of 10 flowers of *E. grandiflora* from 10 different plants, I extracted 135 small insects of the following lengths:— 0–1 mm (6), 1–2 mm (99), 2–3 mm (24), 3–4 mm (5) and 4–5 mm (1). Except perhaps for the largest, of 4–5 mm, these are all of a size suitable for a small or medium-sized hummingbird, since they have a similar size distribution (but with a peak at 1–2 mm instead of 2–3 mm) to the insects collected from the crop contents of the larger hummingbird *O. estella* by Carpenter (1976). In August and September 1978, Dr. H. Sturm *(in lit.)* collected 1035 small insects from 52 flowers of *E. corymobosa* (mean, 20 per flower), and 37 insects from 2 flowers of *E. grandiflora* (mean, 18.5 per flower). Thus the sample which I collected was not unusually large.

Further, I saw *Chalcostigma* feeding in exactly the same way at dead, blackened flower heads of espeletia, which certainly provide neither nectar nor pollen but do contain insects. The common small furnariid of the open páramo, *Leptasthenura andicola,* undoubtedly an insectivore, clings to espeletia flowers and probes the discs in just the same way as the hummingbirds. I therefore conclude that the hummingbirds probe the flower heads for insects and that, when the flowers are available, they are the richest source of small insects for a hummingbird and one that is available in all weathers.

Other methods of foraging

Especially when the weather was fine, *Oxypogon* and *Chalcostigma* frequently hawked for insects in sheltered places, especially in the lea of a bank or cliff or among low bushes growing in sheltered places. Most often I saw them hawking for flying insects between 1 and 3 m above the ground, and occasionally gleaning insects from the twigs and leaves of shrubs. Twice I saw *Chalcostigma* gleaning from rock faces, and 4 times I saw *Oxypogon* clinging to rock faces and collecting something that was too small to see. *Ramphomicron* also hawked for insects frequently, especially (in the cases observed) from higher tree tops along woodland edge.

In comparison with the 2 main methods of insect-foraging, from espeletia flowers and by hawking and gleaning, the short-billed hummingbirds were taking very little nectar. I never saw *Oxypogon* visit any flower except espeletia, in spite of watching birds for minutes on end when they were insect-foraging within a short distance of clumps of *Castilleja fissifolia* and other suitable flowers. *Ramphomicron* was once seen to make a brief visit to the small mauve flowers of *Geranium hirtum,* which lack a corolla tube, and can hardly be an important nectar source. I did not see *Lesbia* visit flowers on the open páramo, though they do so regularly at lower elevations. *Chalcostigma,*

however, visited flowers quite frequently. I had records for 3 kinds of small ericaceous shrubs (*Pernettya* and *Gaultheria*), *Bartsia santolinaefolia, Rubus* cf. *gachetensis,* and *Castilleja fissifolia*; all were more or less brief visits, interspersed between longer bouts of insect-foraging. These flowers are all small (corolla tubes 5–12 mm) and cannot provide large quantities of nectar.

Other observations on *Oxypogon guerinii*

At just after 06.00 hours in the morning of 5 September, in cloud and driving rain and with an air temperature of about 4° C, I watched 2 males of *Oxypogon* foraging on the open páramo fully exposed to the weather. In conditions of poor visibility my attention was drawn to them by hearing a squeaky monosyllable, *seep,* repeated at intervals of about 3 seconds. Thinking that it might be a young bird food-begging I approached the sound, to find that in both cases it was a male *Oxypogon* calling from low perches on the espeletias between bouts of feeding from the flower discs. The 2 birds were just in auditory contact, and both were foraging within restricted areas. Later, I heard another calling in the same way in another part of the páramo. Other observations indicated that individuals coming into contact with one another on the open páramo behave aggressively, and it seems most probable that the calling males were advertising their ownership of a feeding territory. The persistence of the calling in such adverse conditions is otherwise hard to interpret.

I did not see female *Oxypogon* behaving in this way, and in fact saw them only in more sheltered places along cliff faces and in gullies. In one such place, under a rock overhang, one of the students of the party with whom I was camping on 4 September drew my attention to a nest attached to dry vegetation hanging from the ceiling of the cave. It proved to be a nest of *Oxypogon* containing 2 eggs, which a female was incubating. About 4 m away, also attached to vegetation hanging from the cave roof, was another nest, empty but in good condition. On the following day, as this second nest was still empty and we had to leave the area, I collected it for the Museo de Historia Natural of the Universidad Nacional de Colombia.

The nests were extremely large for the size of the bird; both were bulky cups of similar construction, and were suspended in the same way, being attached on one side to the supporting vegetation. The collected nest had the following dimensions: external diameters 93 and 79 mm (i.e. oval, not circular in plan), external depth 75 mm, diameter of cup 32 mm, depth of cup 24 mm. It was very light for its size, weighing 10.5 g. It was constructed of moss externally, with a thick and dense lining of a pale, soft material which on later examination proved to be matted "wool" from the leaves or inflorescences of espeletia. In fact, a careful search of the surrounding vegetation had shown that there was no other plant that could have provided material of this kind. The thickness of the nest lining, as measured round the rim of the cup, varied from 12 to 20 mm. Puzzlingly, no cobweb could be seen on the surface of the nest, which appeared to be attached to the hanging twigs of a small dry shrub by some longer strands of vegetable fibres that were embedded in the nest and entwined among the stems of the supporting plant. Consequently the nest came away very easily when pulled.

Oxypogon was seen several times interacting with *Chalcostigma*; on all occasions it was displaced, and sometimes chased, by the larger species. Once

a female *Oxypogon* was seen to attack and chase a male *Ramphomicron* which intruded in an area, close to a cliff face, where the *Oxypogon* had been perching and feeding and which it may have been defending as a feeding territory and potential nesting territory. In all these encounters dominance was strictly in order of size.

Discussion

These observations show that the 4 short-billed hummingbirds were, at the time of my visits, depending heavily on espeletia flowers for their food supply, and suggest that *Oxypogon* could not have built an effective nest without "wool" from the espeletias. How general is the dependence of páramo hummingbirds on the genus *Espeletia*? A review of the scanty data from other sources throws some light on the question.

Food and feeding habits. No quantitative data are available, but it seems that *Oxypogon* and *Chalcostigma* are very largely, at times probably exclusively, insectivorous. Dorst (1956) reported that *Chalcostigma olivaceum* was entirely insectivorous in an area of puna in Peru, during the period of his study, as there were no suitable flowers available to it. At times both *Oxypogon* and *Chalcostigma* regularly forage for insects on the ground. Ruschi (1961, 1973) has described how *Oxypogon* may spend the greater part of the day foraging on the grass, walking and making small forward and sideways jumps to take small insects. Vuilleumier (1969) has observed *Chalcostigma olivaceum* in the Bolivian Andes walking about on densely matted grass, picking up insects, and cited similar observations for *C. stanleyi* in Ecuador. Terrestrial foraging has apparently not been recorded for *C. heteropogon,* probably for lack of observations in the right circumstances. I never saw it or *Oxypogon* behaving in this way. It seems probable that probing for insects in espeletia flower heads is a more efficient way of foraging, and that when these flowers are available in quantity the hummingbirds do not resort to ground-feeding.

Vertical (altitudinal) movements have been reported for several Andean hummingbirds, but they are little understood. Vuilleumier & Ewert (1978) quote P. Schwartz as noting that in northwestern Venezuela *Oxypogon* is seldom, if ever, seen in open páramo vegetation outside the main flowering season (apparently August-November), but do not mention its visiting espeletia flowers. Schwartz found a young bird just out of the nest in mid-December. At times *Oxypogon* is recorded at considerably lower levels, well below the páramo zone. These facts suggest that *Oxypogon* may undertake vertical migrations, perhaps only over short distances, ranging up into the páramo, and breeding there, when the espeletia flowers provide an abundant supply of insect food.

A short, sharply pointed bill is clearly efficient for probing espeletia flowers; but this kind of bill cannot have evolved as a specific adaptation to espeletias. All the Colombian hummingbirds with bills of this kind have ranges that are wider than the range of espeletias, in some cases much wider. Other species of *Chalcostigma* with bills similar to that of *C. heteropogon* occur well to the south of the range of espeletias. Dorst (1956) reported that *C. olivaceum* often probes for insects among the thick mat of hairs that covers the cushion cacti *Opuntia lagopus* and *O. floccosa*. Probably a short, sharp bill is generally efficient for picking and probing for insects in thickly clustered or

matted vegetation of many different types, so that hummingbirds with this kind of bill were pre-adapted to exploit the concentrated insect food provided by espeletia flowers.

A short, straight bill also fits the small flowers with short corolla tubes that are characteristic of páramo vegetation. Caution is needed, however, in interpreting this matching of bill and flower as co-evolutionary; and in particular it needs to be known whether or not the hummingbirds are the main pollinators of the flowers.

Nesting. The first account of the nesting of *Oxypogon* was given by Rusch (1961), who found several nests in the Andes of northwestern Venezuela. His description indicates that they were similar to the nests described here, being thickly lined with white wool from a species of espeletia, *E. schultzii*, and they were also placed under rocky overhangs. A very similar kind of nest, placed in similar sites, is built by *Oreotrochilus estella*, which nests at very high altitudes in the puna zone of Peru and neighbouring countries (Dorst 1956, Carpenter 1976); but in the puna (where espeletias are absent) the nests are insulated mainly with the wool of alpacas, llamas and domestic sheep, material which is not available in the northern Andes where *Oxypogon* breeds. Hence it might be concluded that espeletias are essential for any hummingbird nesting on the open páramo. There must, however, be alternative materials in some areas since, as already mentioned, espeletias do not occur in some parts of the Colombian Andes, nor in the Santa Marta massif, where *Oxypogon* occurs and undoubtedly breeds. Perhaps the most likely alternative is the wool from the leaves of *Senecio*, a widespread composite genus of which some Andean species are superficially rather similar to espeletias.

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